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DANIEL PEREIRA MONTEIRO

**Efeito das mudanças de uso do solo sobre assembleias de besouros rola-bostas
(Scarabaeinae: Coleoptera) na Amazônia brasileira**

Belém
2024

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, do convênio Universidade Federal do Pará e Embrapa Amazônia Oriental, como requisito parcial para obtenção do título de Mestre em Ecologia.

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*“[...]Permita que eu fale
Não as minhas cicatrizes
Elas são coadjuvantes
Não, melhor, figurantes
Que nem devia tá aqui
[...]
Por fim, permita que eu fale
Não as minhas cicatrizes
Achar que essas mazelas me definem
É o pior dos crimes
É dar o troféu pro nosso algoz e fazer
nóis sumir*

*Tenho sangrado demais
Tenho chorado pra cachorro
Ano passado eu morri
Mas esse ano eu não morro[...]*”

Emicida - AmarElo

Efeito das mudanças de uso do solo sobre assembleias de besouros rola-bostas (Scarabaeinae: Coleoptera) na Amazônia brasileira

RESUMO

Nas regiões tropicais, o ecossistema amazônico se destaca como uma das áreas mais biodiversas do planeta. No entanto, a Amazônia tem sofrido intensas mudanças no uso do solo. Apesar dos avanços no conhecimento proporcionados por estudos anteriores sobre como a biodiversidade amazônica responde às atividades humanas, nossa capacidade de informar práticas de conservação e políticas na região ainda é limitada por algumas lacunas de conhecimento-chave. Aqui, nosso objetivo é abordar algumas dessas lacunas de conhecimento investigando como os besouros rola-bosta respondem às mudanças no uso do solo na Amazônia brasileira. Para isso, empregamos modelos lineares de efeitos mistos para analisar os efeitos das mudanças no uso do solo nas estimativas de riqueza de espécies e abundâncias de besouros rola-bosta em nível de local, a partir de um conjunto de dados da Amazônia brasileira. Nossas descobertas demonstram que a conversão da floresta amazônica resultou em declínios na biodiversidade de besouros rola-bosta. Esses declínios seguiram um gradiente de sistemas menos a mais antropogênicos e foram mais pronunciados para a riqueza de espécies de besouros rola-bosta do que para a abundância. Além disso, demonstramos que a riqueza de besouros rola-bosta diminuiu após perturbações florestais e conversão para outros sistemas florestais e não florestais. Embora tenhamos obtido resultados consistentes do efeito negativo das mudanças de uso do solo na riqueza, também discutimos que nossas observações apontam para a existência de outros fatores importantes das respostas dos besouros rola-bosta. De maneira geral, nosso estudo demonstra o impacto significativo das mudanças no uso do solo nos besouros rola-bosta amazônicos e reforça a necessidade, para além da conservação de florestas primárias, a adoção de sistemas produtivos que suportem uma maior biodiversidade.

Palavras-chave: floresta tropical; biodiversidade de insetos; plantações exóticas; degradação do habitat; cobertura do solo

Effect of land use changes on dung beetle assemblages (Scarabaeinae: Coleoptera) in the Brazilian Amazon

ABSTRACT

Across the tropical regions, the Amazonian ecosystems stand out as one of the most biodiverse areas on the planet. However, Amazonia has undergone intense land-use changes. Despite knowledge advances provided by previous studies on how Amazonian biodiversity respond to human activities, our capacity to inform conservation practices and policy in the region is still limited by some key knowledge gaps. Here, we aim to tackle some of these knowledge gaps by investigating how dung beetles respond to land use changes across the Brazilian Amazon. To do so, we employed mixed-effects linear models to analyzed land use changes effects on site-level estimates of dung beetle species richness and abundances from a dataset of Brazilian Amazon. Our findings demonstrating that Amazonian forest conversion resulted in dung-beetles biodiversity declines. These declines followed a gradient from less to more anthropogenic systems and were more pronounced for dung beetle species richness than for abundance. Beyond, we demonstrate that dung beetle richness decreases following forest disturbances and conversion to other forest and non-forest systems. Although we obtained consistent results of the negative effect of changes on richness, we also discuss that our observations also point to the existence of other important drivers of dung beetle responses. Overall, our study demonstrates the significant impact of land use changes on Amazonian dung beetles and reinforces the need, in addition to the conservation of primary forests, for the adoption of productive systems that support greater biodiversity.

Keywords: tropical forest; insect biodiversity; exotic plantations; habitat degradation; land cover

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1. INTRODUÇÃO GERAL

A região tropical concentra a maior parte da biodiversidade do planeta (GODFRAY; LEWIS; MEMMOTT, 1999; NUÑEZ; PAUCHARD, 2010), no entanto a biodiversidade e os processos que governam sua distribuição no tempo e espaço são menos conhecidos nessa região em relação às outras regiões do globo (MARTIN, L. J.; BLOSSEY; ELLIS, 2012). Os trópicos além proporcionalmente serem menos estudados, atualmente enfrentam um acelerado processo de modificação de seus ecossistemas (BARLOW et al., 2018). Sabemos que as alterações antrópicas dos ambientes naturais são a principal causa da perda de biodiversidade no planeta (NEWBOLD et al., 2015). E é previsto que as mudanças no uso do solo, seguidas pelas mudanças climáticas serão as maiores responsáveis pela perda de espécies e modificação nos padrões da biodiversidade (SALA et al., 2000). Diversos estudos têm documentado os efeitos adversos dessas mudanças sobre a biodiversidade (ALLAN et al., 2015; MAITIMA et al., 2009; MUMME et al., 2015; NEWBOLD et al., 2015). No entanto, a velocidade em que os ambientes são modificados e a biodiversidade perdida, é maior que a velocidade em que esse conhecimento é acumulado (BALMFORD; BOND, 2005).

Entre os ecossistemas terrestres, as florestas tropicais se destacam por sua complexidade, extensão e biodiversidade, abrigando mais da metade das espécies conhecidas no planeta (GIBSON et al., 2011). A floresta Amazônica além de ocupar o posto de maior floresta tropical, é uma das mais relevantes florestas do mundo. A região abriga uma das maiores diversidades de espécies, desempenhando um papel crucial na manutenção da biodiversidade a nível global (BOUBLI; HRBEK, 2012; PARRON et al., 2019). Contudo, nas últimas quatro décadas o percentual de área da Amazônia convertidos em usos do solo antrópicos cresceu de 6% para 15% em 2020 (SOUZA et al., 2020). As taxas de desmatamento flutuam ao longo dos anos e a perda da vegetação original varia entre os países onde o ecossistema ocorre, no entanto permanecem entre as maiores taxas entre as regiões florestais do mundo (KIRBY, K. R. et al., 2006; SOUZA et al., 2020). No Brasil, país que detém cerca de 60% da Amazônia, a substituição da cobertura florestal já alcança 19% do ecossistema (SOUZA et al., 2020), avançando principalmente a partir do chamado arco do desmatamento. As áreas desmatadas são destinadas principalmente para atividades econômicas de larga escala (ex. pecuária, agricultura, imobiliária e/ou mineração (FRANCO et al., 2019; LAPOLA et al., 2023; MARTINS et al., 2022; SOUZA et al., 2020), representando uma das principais ameaças à biodiversidade amazônica (FEARNSIDE, P., 2017). Além disso, a construção de infraestrutura de transporte e energia são conhecidos facilitadores das mudanças de uso do solo na Amazônia (KIRBY, K. R. et al., 2006; PFAFF et al., 2007). Desse modo, diante dos desafios da conservação da biodiversidade, a compreensão da resposta das comunidades biológicas às mudanças ambientais na

Amazônia é fundamental para auxiliar na implementação de medidas de monitoramento de impacto ambiental, contribuindo assim com atividades de proteção e manejo sustentável da biodiversidade.

Diversos impactos negativos da conversão de florestas primárias em áreas agrícolas são relatados para diferentes grupos de organismos (KIRBY, K. R. et al., 2006; LAPOLA et al., 2023; LAURANCE, W. F. et al., 2018; PFAFF et al., 2007). Apesar desses estudos evidenciarem as perdas da biodiversidade na Amazônia, algumas lacunas de conhecimento limitam a nossa capacidade de informar políticas ambientais e práticas de conservação (CARVALHO et al., 2023; FONSECA, C. R.; VENTICINQUE, Eduardo Martins, 2018). Grande parte dos estudos é realizada em localidades únicas (por exemplo, em um ou poucos municípios geograficamente próximos ou em uma Unidade de Conservação e áreas degradadas próximas), o que limita nossa capacidade de compreender o impacto das mudanças no uso do solo numa escala espacial maior (CARVALHO et al., 2023). Além disso, a maioria das pesquisas anteriores de alta abrangência espacial focaram em vegetação (FLORES et al., 2024; STEEGE et al., 2015), o que limita nossa compreensão sobre os impactos das mudanças no uso do solo em níveis tróficos mais elevados. Buscamos aqui avaliar um conjunto de dados de larga escala territorial e que contempla um amplo espectro de classes de uso do solo, a fim de melhor compreender os efeitos das mudanças no uso do solo na biodiversidade amazônica.

Para nosso estudo escolhemos os besouros escarabeíneos (Scarabaeidae: Scarabaeinae) como grupo focal. A maioria das espécies de escarabeíneos se alimentam de detritos, como carcaças de animais, fungos, matéria vegetal em decomposição e, principalmente, excrementos de vertebrados (HALFFTER, G.; HALFFTER, V., 2009; HOLTER; SCHOLTZ, 2007). Através de seus hábitos e estratégias de alimentação e nidificação esses besouros desempenham importantes funções nos ecossistemas tropicais (HALFFTERS; EDMONDS, 1982; NICHOLS et al., 2008). As espécies coprófagas podem promover a dispersão secundária de sementes (ANDRESEN, 2001; GRIFFITHS et al., 2016) e o controle de populações de dípteros e vermes patógenos presentes no esterco de herbívoros (BORNEMISSZA, 1970). Espécies que escavam túneis para enterrar/alocar seus recursos, seja para alimentação ou nidificação, promovem a bioturbação do solo, influenciando a porosidade e melhorando a aeração e infiltração de água (BROWN et al., 2010). Além disso o consumo de esterco e materiais em decomposição incorpora uma série de elementos químicos ao solo e nas cadeias tróficas (MALDONADO et al., 2019; YAMADA et al., 2007).

Além de seu papel ecológico, os escarabeíneos são um grupo de insetos com alta riqueza especialmente nos trópicos (SLIPINSKI; LESCHEN; LAWRENCE, J. F., 2011; VAZ-DE-MELLO, 2022) e apresentam uma série de características que permitem que sejam utilizados para avaliar efeitos de distúrbios antrópicos em estudos ecológicos. Por exemplo, Spector, 2006 enfatiza seis

parâmetros que favorecem o uso de besouros escarabeíneos como bons indicadores ambientais: i) facilidade na coleta e padronização da amostragem; ii) taxonomia acessível e bem resolvida; iii) ampla distribuição geográfica; iv) resposta rápida a mudanças ambientais; v) importância ecológica e vi) correlação com outros táxons (por exemplo vegetação e mamíferos). Esses fatores são evidenciados por diversos estudos demonstrando que os Scarabaeinae são sensíveis a alterações na cobertura vegetal (GÓMEZ-CIFUENTES et al., 2020; SILVA, R. J.; DINIZ, S.; VAZ-DE-MELLO, 2010), nas características ambientais (NICHOLS et al., 2007; RIVERA; SILVA, P. G. Da; FAVILA, Mario E., 2021) e nas comunidades de mamíferos (BOGONI; SILVA, P. G.; PERES, 2019; CULOT et al., 2013).

Diferentes estudos têm investigado as implicações das mudanças no uso da terra nas comunidades de Scarabaeinae (FUZESSY et al., 2021; LÓPEZ-BEDOYA et al., 2022; NICHOLS et al., 2007), e embora relatem uma tendência geral de redução na riqueza e abundância de besouros em ambientes perturbados, em alguns casos, essas respostas são heterogêneas. A conversão de ambientes florestais para ambientes abertos reduz a riqueza de espécies e a abundância de especialistas em florestas. Ainda assim, especialistas em habitats abertos podem se beneficiar dessas mudanças e exibir maiores abundâncias (ALONSO, Celeste B. Guerra; ZURITA, Gustavo A.; BELLOCQ, 2022; ALONSO, Celeste Beatriz Guerra; ZURITA, Gustavo Andrés; BELLOCQ, 2020; GÓMEZ-CIFUENTES; MUNÉVAR; ZURITA, G., 2023). Além disso, apesar de sabermos que as diferenças regionais como clima e tipo de vegetação original também determinam a variação na resposta entre ecossistemas e continentes (FUZESSY et al., 2021; PHILLIPS; NEWBOLD; PURVIS, 2017), a compreensão dessas especificidades em relação aos ecossistemas sulamericanos como a Amazônia, ainda é pontual. Compreender como as mudanças no uso da terra afetam as assembleias de Scarabaeinae ao longo da região amazônica constitui uma importante ferramenta para elaborar estratégias de monitoramento da biodiversidade cada vez mais eficazes considerando as particularidades desse ecossistema.

Com base nesses conhecimentos, o objetivo da minha dissertação é preencher lacunas na nossa compreensão sobre os impactos das mudanças do uso do solo na riqueza e abundância de insetos da Amazônia. Para isso trabalhamos com uma base de dados besouros rola-bosta na Amazônia brasileira e construímos modelos lineares de efeito misto, a fim de compreender como esses organismos respondem a um gradiente de usos do solo. A dissertação é apresentada em capítulo único e estruturado em forma de artigo, onde apresentamos e discutimos os efeitos das mudanças de uso do solo sobre riqueza e abundância de escarabeíneos amazônicos.

2. CAPÍTULO ÚNICO

Do changes in land use drive the decline of dung beetles (Coleoptera: Scarabaeinae) across the Brazilian Amazon?

A dissertação foi elaborada e estruturada em capítulo único, no formato de artigo, e apresentada aqui em língua inglesa conforme as normas da revista científica *Forest Ecology and Management*, a qual será submetido. As normas da revista estão disponíveis em: <https://www.sciencedirect.com/journal/forest-ecology-and-management/publish/guide-for-authors>.

ARTIGO

Do changes in land use drive the decline of dung beetles (Coleoptera: Scarabaeinae) across the Brazilian Amazon?

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ABSTRACT

Across the tropical regions, the Amazonian ecosystems stand out as one of the most biodiverse areas on the planet. However, Amazonia has undergone intense land-use changes. Despite knowledge advances provided by previous studies on how Amazonian biodiversity respond to human activities, our capacity to inform conservation practices and policy in the region is still limited by some key knowledge gaps. Here, we aim to tackle some of these knowledge gaps by investigating how dung beetles respond to land use changes across the Brazilian Amazon. To do so, we employed mixed-effects linear models to analyzed land use changes effects on site-level estimates of dung beetle species richness and abundances from a dataset of Brazilian Amazon. Our findings demonstrating that Amazonian forest conversion resulted in dung-beetles biodiversity declines. These declines followed a gradient from less to more anthropogenic systems and were more pronounced for dung beetle species richness than for abundance. Beyond, we demonstrate that dung beetle richness decreases following forest disturbances and conversion to other forest and non-forest systems. Although we obtained consistent results of the negative effect of changes on richness, we also discuss that our observations also point to the existence of other important drivers of dung beetle responses. Overall, our study demonstrates the significant impact of land use changes on Amazonian dung beetles and reinforces the need, in addition to the conservation of primary forests, for the adoption of productive systems that support greater biodiversity.

Keywords: tropical forest; insect biodiversity; exotic plantations; habitat degradation; land cover

2.1. INTRODUCTION

Habitat loss represent one of the primary drivers of global biodiversity decline (Newbold et al., 2015). Agricultural expansion, overexploitation of natural resources, and other forms of land transformation have significantly contributed to the fragmentation and loss of natural habitats, resulting in substantial and widespread changes in biodiversity (Haines-Young, 2009). It is estimated that land use change impacts on biodiversity will surpass the influence of climate change and species introductions by 2100 (Chapin et al., 2000; Sala et al., 2000). Several studies have documented the adverse effects of land use changes on biodiversity, leading to reductions in various diversity metrics

across different ecosystems and regions of the world (Allan et al., 2015; Ewers et al., 2015; Maitima et al., 2009; Mumme et al., 2015). Understanding organisms' responses to habitat modifications is crucial for preventing and mitigating biodiversity declines, especially in the tropics, which harbor the majority of global biodiversity (Barlow et al., 2018; Gibson et al., 2011; Nuñez and Pauchard, 2010). Safeguarding tropical biodiversity is key for achieving global conservation goals (Magurran and Dornelas, 2010). Tropical forests alone harbor more than half of the planet's known species (Barlow et al., 2018; Godfray et al., 1999). However, the rapid and increasing transformation of tropical environments is threatening biodiversity and associated ecological processes that are key for ecosystem stability and human well-being (Cardinale et al., 2012; Hasan et al., 2020; Sales et al., 2020). In this context, investigating the ecological impacts of human activities on tropical biodiversity becomes crucial for the development of effective conservation strategies and policy in the tropics.

Amazonia has undergone recent and intense land use changes, notably due to the expansion of agriculture and livestock farming, mining activities, and logging (Fearnside, 2017; Lapola et al., 2023). Deforestation rates fluctuate over the years and the losses of original vegetation varies between countries where the ecosystem occurs, however, they remain among the highest rates among forested regions in the world (Kirby et al., 2006; C. M. Souza et al., 2020). In Brazil, that have approximately 60% of the Amazon, forest cover replacement has already achieve 19% of the ecosystem (C. M. Souza et al., 2020), advancing mainly from the so-called arc of deforestation. Additionally, infrastructure construction, such as roads and hydropower dams for energy generation, contributes to habitat fragmentation and loss, even within protected áreas (Kirby et al., 2006; Laurance et al., 2018; Pfaff et al., 2007). Recent studies highlight that human-driven disturbances have been affected Amazonian biodiversity and fundamental ecosystem processes, with changes in the structure and composition of Amazonian biological communities, even within areas considered intact (Barlow et al., 2016; Franco et al., 2019; Griffiths et al., 2016; Laurance et al., 2018; Sales et al., 2020).

Despite knowledge advances provided by previous studies on how Amazonian biodiversity respond to human activities (Aleixandre-Benavent et al., 2018; Lapola et al., 2023), our knowledge in this region is still limited by some important gaps (Carvalho et al., 2023b; Shennan-Farpón et al., 2021). First, most large-scale research on human-driven impacts for Amazonian biodiversity has been focused on vegetation (e.g. Flores et al., 2024; Steege et al., 2015). This limitation both reflects the lack of large-scale data integration for other Amazonian taxa at higher trophic levels (Carvalho et al., 2023b; Fonseca and Venticinque, 2018; Parron et al., 2019) and limits our capacity of understanding how other biodiversity groups might be affected by anthropogenic activities. Second, most studies assessing the ecological impacts of land-use change for fauna communities has been conducted in a single or a few areas (e.g. a single conservation unit in contrast to a degraded area; Decaëns et al.,

2018; Gardner et al., 2008; Silva et al., 2024). This geographical bias limits our understanding of how Amazonian fauna biodiversity might be changing across the ecosystem. Finally, a recent study shows that ecological research in Amazonia has been biased towards undisturbed forests (Carvalho et al., 2023b), which highlights the need for a large-scale assessment of how land-use change affects Amazonian fauna biodiversity.

Here, we aim to tackle these knowledge gaps by investigating how dung beetles (Coleoptera: Scarabaeinae) respond to land use changes across the Brazilian Amazon. To do so, we analyzed site-level comparisons of dung beetle species richness and abundances across a gradient of land use categories from the scientific literature stored in the TAOCA database (<https://www.taoca.net/>; Carvalho et al., 2023). Our database includes snapshot samples of dung beetle assemblages from different sites across the Brazilian Amazon, enabling spatial comparisons of samples under contrasting land-use conditions. We focused on dung beetles given their relevance for key ecological processes (Nichols et al., 2008) and sensitivity to environmental changes (Gómez-Cifuentes et al., 2020; Silva et al., 2010). For instance, previous research has demonstrated the importance of dung beetles for seed dispersal, nutrient cycling, soil bioturbation and other key processes for ecosystem maintenance (Andresen, 2001; Brown et al., 2010; França et al., 2018; Griffiths et al., 2016). Previous meta-analytical research has also demonstrated that primary forest loss and degradation reduce dung beetle biodiversity and associated ecological processes (e.g. Fuzessy et al., 2021; Nichols et al., 2007). Yet, these previous assessments (i) are mostly based on comparisons of effect size, extracted from the literature, between land use classes and mean dung beetle abundance and richness, and (ii) found dung beetle responses to land use changes being heterogeneous and dependent on geographical context. We tackle these limitations by using a raw dataset of dung beetles collected across Brazilian Amazon between 2008 and 2020.

From this dataset, we determined site-level estimates of dung beetle species richness and total abundance and employed mixed-effects linear models specified to test two main hypotheses: First, land use change lead to declines in Amazonian dung beetle species richness and abundance which follow a gradient of environmental alteration, ranging from higher abundance and richness within primary undisturbed forests to intermediate and lower levels within disturbed forests and agricultural lands, respectively. This hypothesis builds on previous research demonstrating dung beetles' high sensitivity to environmental changes (França et al., 2019; Fuzessy et al., 2021; Machado et al., 2023; Ríos-Touma et al., 2023), which are more subtle within primary disturbed forests than in agricultural and pasture lands (Decaëns et al., 2018; Nichols et al., 2007; Rivera et al., 2021). Finally, although declines are observed for both dung beetle responses, different decreases will be observed for species richness than abundance. Despite the negative impacts environmental changes can bring to

biodiversity (e.g. Franco-Rozo et al., 2024; Souza et al., 2020), previous research has shown that small-bodied species can thrive in disturbed ecosystems (Nichols et al., 2013; T. B. Souza et al., 2020), balancing abundance while there is a more pronounced loss in the richness of large-bodied species (Bernardino et al., 2024).

2.2. METHODS

2.2.1. Data Collection:

Our study builds on the literature search and inclusion criteria established within the SYNERGIZE (Synthesising Ecological Responses to Degradation In Amazonian Environments) project (see details in Carvalho et al. 2023) and datasets stored within the TAOCA platform (<https://www.taoca.net>). The TAOCA platform aggregates data from the published literature for different terrestrial and freshwater biodiversity groups in the Brazilian Amazon, including dung beetles. Only ecological community datasets from studies (i) adopting quantitative and repeatable sampling protocols, (ii) providing geographical coordinates from sampling sites, and (iii) having dung beetles identified at a minimum of genus level were kept at our analysis. Besides ecological community datasets, TAOCA also provides site-level metadata extracted from the literature and validated by first and/or corresponding authors from each selected study. Metadata includes land use type, geographical coordinates and other methodological details (e.g. trap type, bait type, sampling date, among other information). To assess our hypotheses, sites were grouped into seven major land-use classes (see Table 1).

In total, our analyses uses 12 datasets spanning a total of 12 years (2008 to 2020), which were derived from 29 published studies and sampled at 924 locations from across 23 different areas in the Brazilian Amazon (Figure 1). We defined areas as the territory or geographic region reported as independent within the study where datasets obtained from. For example, when a study compared two or more independent areas, we considered those as distinct areas in our analyses. We also filtered TAOCA datasets by trap and bait methodologies, analyzing datasets (i) adopting only pitfall traps baited with omnivore dung (Marsh et al., 2013), (ii) with standardized sampling methods within two or more land-use classes per area/study, and (iii) similar sampling efforts across land-use classes.

2.2.2. Assemblage Data:

The dataset consisted of a list of individuals, classified as 162 species and 351 morphospecies (e.g., *Ateuchus* sp1, *Ateuchus* sp2...) or *affinis* (e.g., *Ateuchus* aff. *candezei*). We maintained TAOCA's classification and referred to morphospecies and *affinis* as distinct taxa in our dataset

because it was not possible to reliably combine taxa from different studies (e.g., *Ateuchus* sp1_A from database A and *Ateuchus* sp1_B from database B). We calculated species richness and total abundance for each location and land use. We corrected raw abundance measures for the sampling effort expended at each location (e.g. number of pitfalls per transect) and sampling time (e.g. days of trap in the field), rescaled abundance. To avoid introducing additional heterogeneity into the modelled values, we rescaled the local effort and sampling time so that the most sampled location had a value of one. Then, we divided study-level raw abundance values by relative sampling effort (relative effort = rescaled local effort x rescaled sampling time) following a similar approach from previous research (Newbold et al., 2015).

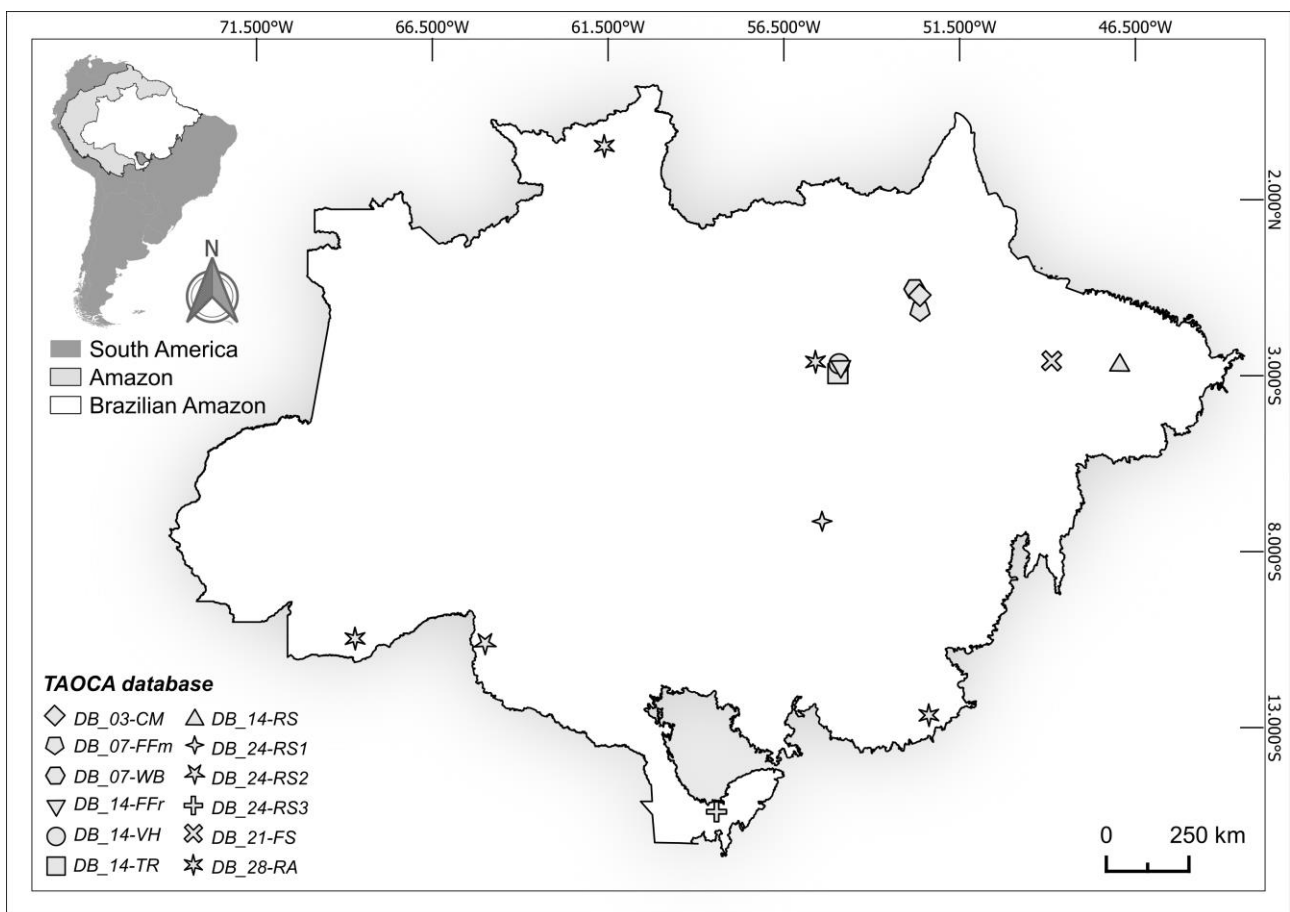


Figure 1: Geographical distribution of dung beetle datasets in Brazilian Amazon.

2.2.3. Environmental Data:

Our study focuses on dung beetle responses to land use changes. TAOCA metadata provided by the first and/or senior authors from each study contained 71 different categorical land use descriptors, which we grouped into seven land use classes following a gradient of increasing modification (Nichols et al., 2007; Fuzessy et al., 2021): primary forests, selective logging, burned forest, secondary forest, silviculture, agriculture, and pasture (see details in Table 1).

Table 1: Land use classes defined for the analyzes.

Land use class	Description of grouped categories	Number of sampling sites
Primary forest	Undisturbed primary forests; forest corridors and edges; forests with small-scale hunting or extractivism	263
Selective logging	Primary forests with selective logging at different removal intensities	139
Fire	Primary forests with and without disturbance or secondary forests affected by fire	176
Secondary forest	Abandoned plantations and areas with passive recovery; areas with active and/or natural recovery with human intervention	102
Silviculture	Native/exotic tree plantations for wood or fruit production	98
Croplands	Native/exotic herbaceous plantations with short and/or annual cycles	41
Pasture	Exotic pastures for livestock farming	105

2.2.4. Data Analysis:

We addressed our three hypotheses by fitting two linear mixed-effect models (LMEM) using the packages ‘lme4’ (Bates et al., 2015) and ‘lmerTest’ (Kuznetsova et al., 2017). In the first LMEM, we tested the fixed effect of land use, sampling year and relative effort on dung beetle species richness. In the second LMEM, we tested the fixed effect of land use and sampling year on rescaled dung beetle abundance – we did not include relative effort in this model as abundance was previously adjusted for sampling effort. The sampling year was included as a fixed effect in the models in order to isolate its contribution to data variability, avoiding additional noise. Both LMEMs included study area as a random effect to ensure the intercept has a blocking factor accounting for multiple observations from the same study area and methodological differences between areas. We calculated the conditional (R^2_c) and marginal (R^2_m) coefficients of determination for each model using the ‘MuMIn’ package (Bartoń 2023). The R^2_c allows evaluating the model's capacity to explain data variability considering both fixed and random effects, while R^2_m values demonstrate the independent explanatory power of fixed effects.

We also used the ‘partR2’ package (Stoffel et al., 2021) to decompose the variation explained by the fixed effects (R^2_m) relative to each of the included independent variables, which enabled us to assess the relative contribution of each independent factor in explaining changes in dung beetle richness and rescale abundance. After the LMEMs, we conducted pairwise contrast to test our hypothesis that dung beetle declines will follow a gradient of environmental alteration, ranging from higher abundance and richness within primary undisturbed forests to intermediate and lower levels within disturbed forests and agricultural lands, respectively. We used natural base logarithmic and

square root transformations for abundance and richness, respectively, to correct and meet the model assumptions. The normality and homoscedasticity assumptions of the data were confirmed by visual inspection residual and quantile plots (detailed in appendix A). All analyses were conducted in the R software (R Core Team, 2023).

2.3. Results

Species richness varied significantly across land-use classes (Figure 2.A), ranged from one single species per sampling unit (within a pastureland) to 55 species (within a primary forest), while abundances ranged from 1 to 7330 (both numbers from pasturelands). The average richness ranged from 26.6 (SD±9.3) in primary forest to 8.3 (SD±3.5) in pasture, while the average rescaled abundance ranged from 680.7 (SD±1573.2) in pasture to 226.5 (SD±390.5) in silviculture. *Trichillum* sp.1-14 was the most abundant species in pasture and cropland areas, with 34,7% and 30,1% of the total individuals collected in these land uses, respectively; *Ontherus carinifrons* was the most abundant in the in forestry with 20,0% of individuals, *Ateuchus* aff. *latus* in the primary forest with (14,5%), *Onthophagus rubescens* (10,5%) in the selective logging, *O.* aff. *haematopus* (8,3%) in secondary forest and *Canthon fulgidus* (6,8%) in forest affected by fire. The number of traps per sampling unit ranged from 3 to 10 between the different studies, and the time that the traps remained in the field ranged from 1 to 7 days.

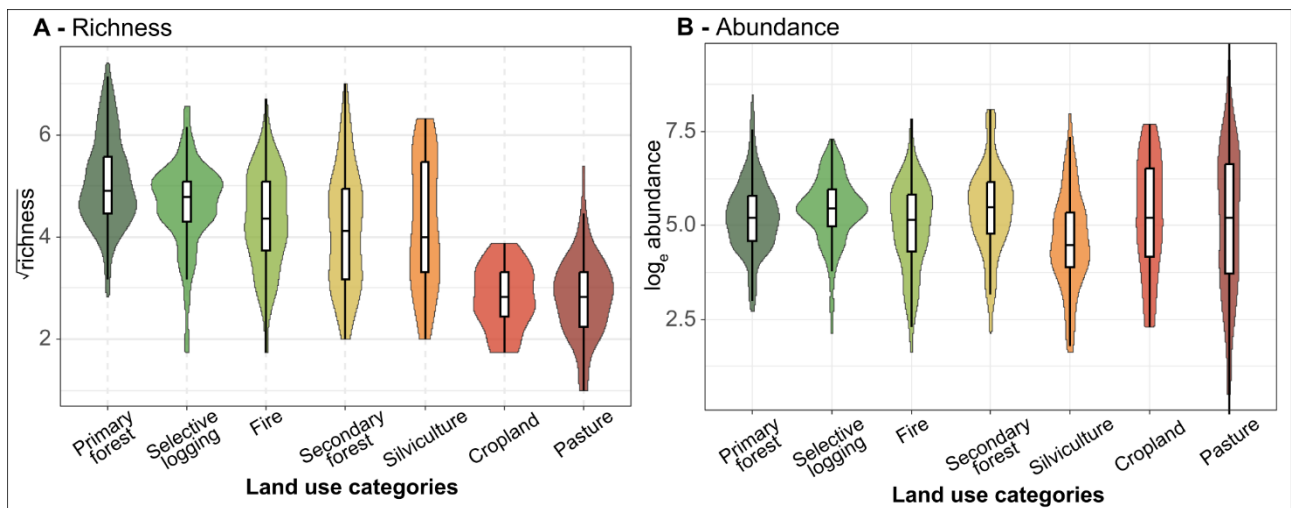


Figure 2: Distribution of log of abundance and square root of species richness of Amazonian dung beetles between land use types.

The land use and the sampling year had significant effects on the square root of richness of species of dung beetles, while relative effort did not have significant effect in this richness (LMEM: Table 2). The model explained 72.3% of the observed variation in species richness, with land use, year and relative effort explaining 49.3% of the variability. Land use accounted for 20.0% of the observed variation and sampling year accounted for 14,9%, when marginal R^2 partitioning was

performed. Dung beetle richness declined across our gradient of land use classes (Figures 2.A, 3.A). Except for selective logging, all land uses were statistically different from primary forest and exhibited lower dung beetle richness (Table 3). And the pairwise contrast reveals that pasture and agriculture hold similar levels of richness, while all other land uses are distinct from each other (Figure 3.A, Table 4).

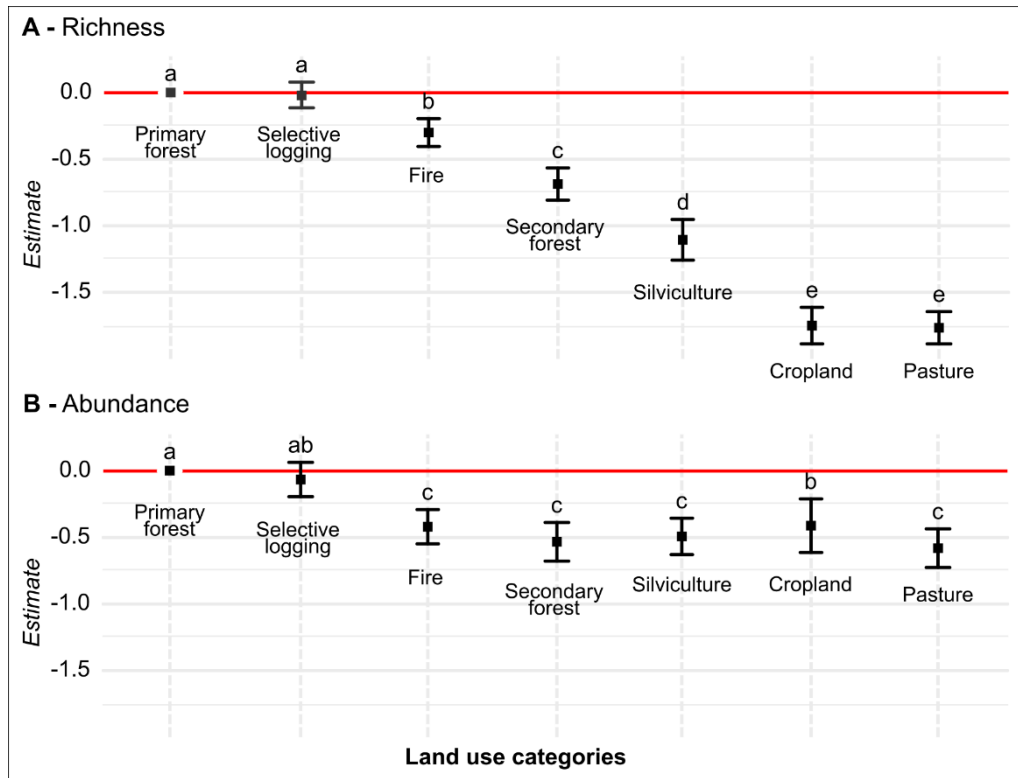


Figure 2: Changes in dung beetle abundance (A) and species richness (B) across different land use classes in the Brazilian Amazon. Different letters represent significant statistical differences ($p < 0.05$). Pairwise contrast and p-values on Table 3.

In abundance of dung beetles, only the fixed effect of land use was significant, while the year did not have a significant effect on the logarithm of the abundance of dung beetles (LMEM: Table 2). Our model explained 44.5% of the observed variation in abundance, with land use and year explaining 17.7%. Land use accounted for only 3% of the observed variation when the marginal R^2 partitioning was performed. Dung beetle abundance also declined with land use change, albeit on a smaller scale than species richness and not following the land use gradient (Figures 2.B, 3.B). Except for selective logging, all land uses hold statistically lower abundance than primary forests (Table 3). Selective logging also exhibited higher abundance than the other categories, except for cropland. And the pairwise contrast revealed two response groups, the first with selective logging and agriculture together showing greater abundance than the second group with the other uses (Figure 3.A, Table 4). Beyond, in both models, the study area as a random effect added a relevant portion to the data variation explained by our models (contrast between R^2_c and R^2_m in Table 2).

Table 2: Result of linear mixed effects model between log of abundance or square root of richness of Amazonian dung beetles as dependent variables; land use, year and relative effort as fixed factor; and area as random factor.

Adjusted Model	R ² m	R ² c	Land-use		Year		Relative effort	
			p-value	dec.R ² m	p-value	dec.R ² m	p-value	dec.R ² m
Model 1 - Richness								
sqrt(Rich)~ LU+ E+ Y + (1 A)	0.493	0.723	<0.001	0.210	<0.001	0.149	0.606	0.000
Model 2 - Abundance								
log(Abd)~ LU+ Y+ (1 A)	0.177	0.445	<0.001	0.026	0.280	0.146	-	-

Note: dec.R²m - decomposed marginal R², LU - land use, E - relative effort, Y - year and A - area. Bold p-values indicate significant differences (LMEM contrast, p < 0.05).

Table 3: Pairwise contrast of log of abundance and square root of species richness of Amazonian dung beetles between primary forest and other land use types after LMEM.

	Richness				Abundance			
	estimate	df	t	p	estimate	df	t	p
<i>Intercept</i>	6.241	24.63	10.128	<0.001	5.673	13.332	8.137	<0.001
Selective logging	-0.026	658.445	-0.286	0.775	-0.074	906.267	-0.579	0.563
Fire	-0.300	661.821	-2.951	0.003	-0.428	907.956	-3.301	0.001
Secondary forest	-0.688	662.786	-5.958	<0.001	-0.540	907.798	-3.653	<0.001
Silviculture	-1.108	653.532	-7.464	<0.001	-0.492	903.853	-3.633	<0.001
Cropland	-1.753	659.366	-12.622	<0.001	-0.417	903.421	-2.099	0.036
Pasture	-1.764	647.255	-15.48	<0.001	-0.588	906.744	-4.067	<0.001

Bold values indicate significant differences between primary forest (*Intercept*) and other land uses (for p-values of the others pairwise comparisons between land uses see Table 4).

Table 4: Pairwise contrast of log of abundance and square root of species richness of Amazonian dung beetles between each land use type after LMEM.

Abundance						
	Primary forest	Selective logging	Fire	Secondary forest	Silviculture	Cropland
Selective logging	0.563					
Fire	0.001	0.009				
Secondary forest	<0.001	0.002	0.427			
Silviculture	<0.001	0.016	0.705	0.799		
Cropland	0.036	0.086	0.962	0.546	0.743	
Pasture	<0.001	<0.001	0.273	0.757	0.603	0.404
Richness						
	Primary forest	Selective logging	Fire	Secondary forest	Silviculture	Cropland
Selective logging	0.685					
Fire	0.002	0.004				
Secondary forest	<0.001	<0.001	<0.001			
Silviculture	<0.001	<0.001	<0.001	0.017		
Cropland	<0.001	<0.001	<0.001	<0.001	<0.001	
Pasture	<0.001	<0.001	<0.001	<0.001	<0.001	0.980

Bold p-values indicate significant differences in species richness between land use pairs (LMEM contrast, p < 0.05).

2.4. Discussion

We performed a large-scale assessment of how primary forest conversion affects Amazonian insect biodiversity, using dung beetles as a study model. Overall, our findings mostly support our research hypotheses, demonstrating that Amazonian forest conversion resulted in insect biodiversity declines. Importantly, these declines followed a gradient from less to more anthropogenic systems and were more pronounced for dung beetle species richness than for abundance.

As primary forests in the tropics are rapidly and progressively converted into other land uses, knowledge about how environmental changes affect insect biodiversity across Amazonia remains largely incomplete (Carvalho et al., 2023b; Fonseca and Venticinque, 2018). Using data from across 23 areas of the Brazilian Amazon, we demonstrate that dung beetle richness decreases following forest disturbances and conversion to other forest and non-forest systems (Figures 2 and 3). This result reinforces the sensitivity of these insects to environmental changes and support previous work showing the influence of habitat conditions and land use change on biological communities (Haines-Young, 2009; Magurran and Dornelas, 2010), including dung beetles both at local and large spatial scales (Bernardino et al., 2024; López-Bedoya et al., 2022; Nichols et al., 2007; Puker et al., 2024). This gradient of richness loss in altered environments have been previously show for dung beetles of different continents, with a few differences on dung beetes responses to habitat modification among tropical zones of Africa, Asia and America (Fuzessy et al., 2021; Nichols et al., 2007). Richness loss might be explained by land-use change impacts on environmental heterogeneity and structure (e.g. canopy cover; França et al., 2018; Gómez-Cifuentes et al., 2020, 2019) and resource availability (e.g. dung provided by vertebrates; Culot et al., 2013; Nichols et al., 2009). Such changes in environmental conditions and resource availability might be more pronounced in crop and pasture lands when compared with forest systems (e.g. selectively logged forests, secondary forests and agroforests), with consequences for environmental filtering processes (e.g. Nunes et al. 2016) and selection of species capable to cope with disturbed ecosystems (Alonso et al., 2022, 2020; Bernardino et al., 2024; Silva et al., 2010).

We found cropland and pasture classes equally bringing the lowest levels of dung beetle species richness. The replacement of native forests by crops and livestock lands for the production of commodities (e.g. soy, corn, beef, and palm oil) is recognized as one of the main drivers of global biodiversity declines, including in Amazonia (Fearnside, 2017; Lapola et al., 2023; Laurance et al., 2001). Although some tropical and sub-tropical dung beetle species might be able to cope with open and drier environments, responses to land-use change might vary between drier and wetter ecosystems – as demonstrated in previous work comparing dung beetles from the Chaco and Atlantic

Forest (Alonso et al., 2022, 2020). Species from closed canopy environments (e.g. tropical moist forest) are not adapted to the adverse conditions of open formations (e.g. savannah and agricultural areas) which have lower humidity, high insolation and greater wind intensity (Klein, 1989). Therefore, many Amazonian forest specialist dung beetles may not be able to cope with higher levels of environmental changes, resulting in the progressive loss of richness and ecosystem processes from forested to agricultural systems (Figure 2; Carrión-Paladines et al., 2021; Decaëns et al., 2018; Reis et al., 2023). Other factors might also explain why pastures, where cattle dung availability might be high, still hold the lowest levels of species richness (Puker et al., 2024; Silva et al., 2014). Besides changes in vegetation structure and feeding/nesting resource availability, pasture management strategies (e.g. agrochemical pollution by pesticides; Bruinenberg et al., 2023; Carvalho et al., 2020; Davis et al., 2004), soil properties (Farias and Hernández, 2017; Laurance, 2007), and changes in microclimatic conditions have been shown to pose strong barriers for forest-specialist dung beetle species (Machado et al., 2023; Puker et al., 2024; Silva et al., 2014).

We observed differences between declines in dung beetle abundance and richness across assessed land uses (Figures 1 and 2), and land-use alone did not explain most of the abundance variability. There are different reasons to explain the different responses between dung beetle richness and abundance. It is likely that other drivers might be affecting abundance responses – e.g. some generalist small-bodied species (e.g. *Trichillum externopunctatum*) can thrive in disturbed ecosystems (Nichols et al., 2013; T. B. Souza et al., 2020), which might buffer the loss of individuals from large-bodied specialist species (Bernardino et al., 2024). Thus, variations in total abundance might be less pronounced than other biodiversity indicators as a result of the abundance turnover between generalist and forest specialist species (Bitencourt et al., 2020; Filgueiras et al., 2015; Massarani, 2013; Quintero and Halffter, 2009) lower variation in abundance across our land uses might also be related to the ability of typical savanna species (eg. *Canthon lituratus*, *C. mutabilis*, *Diabroctis mimas*, *Onthophagus buculos* e *O. hirculos*; Almeida and Louzada, 2009; Tissiani et al., 2017) - to occupy altered environments in the Amazon (Silva et al., 2014). Which may also be the case for invasive species such as the *Digitonthophagus gazella*, an invasive dung beetle species that has been recorded within intra-Amazonian savannas (Matavelli and Louzada, 2008) and savanna ecotones in Brazil (Salomão et al., 2019).

The ecological consequences from human-driven environmental changes on dung beetle assemblages might vary according to local and regional contexts (Fuzessy et al., 2021; Nichols et al., 2007). Regional differences in dung beetle responses land use changes are also consistent with the extinction filter hypothesis, where contemporary biotic responses to environmental changes are conditioned by historical processes (Halffter, 1991; Turvey and Fritz, 2011). Dung beetle richness

declines may be related to the evolutionary history of the Amazonian ecosystems. Throughout the glacial cycles, much of Tropical Americas maintained continuous forest cover (Mayle and Beerling, 2004). Thus, over its evolutionary history, fewer American forest-affiliated dung beetles have been exposed to open vegetation formations (Gill, 1991; Halffter, 1991; Scholtz et al., 2009). This relative stability may have increased the sensitivity of Amazonian dung beetles to forest loss (Halffter, 1991; Scholtz et al., 2009). Investigating the links between dung beetle evolutionary history and responses to land-use change is a key avenue for future research aiming to prevent further insect biodiversity declines across the tropics.

Although we obtained consistent results of the negative effect of changes on richness, our observations also point to the existence of other important drivers of dung beetle responses. Multiple stressors associated with anthropogenic activities – such as loss of heterogeneity and canopy cover (Bitencourt et al., 2020; Carvalho et al., 2023a; Costa et al., 2022; França et al., 2018), impoverished mammal communities (Culot et al., 2013; Feer and Boissier, 2015; Nichols et al., 2009), and changes in soil and climatic characteristics (Carrión-Paladines et al., 2021) – negatively impact resource availability and microclimate conditions for dung beetles. And although we did not observe a significant difference between undisturbed and selectively logged forests, previous research demonstrates that logging impacts on biodiversity — including dung beetles — depends on management methods and intensity of exploitation (França et al., 2016, 2017). Thus, for the maintenance of sensitive species and consequently greater biodiversity, it is fundamental to maintain and protect primary undisturbed forests (Gibson et al., 2011), as well as the proper management of logged areas (e.g. selective logging and extractive activities; França et al., 2024; Moura et al., 2021). The surroundings of these areas should also be maintained or converted into buffer zones with forest land uses to avoid edge effects on protected biodiversity (Costa et al., 2022; Laurance et al., 2018).

Reconciling food production with biodiversity conservation is one of the major societal challenges we currently face. This is particularly so for megadiverse tropical countries and ecosystems such as Brazil and Amazonian region. Our findings reveal that forest systems with higher anthropogenic influence (secondary forest and silviculture) have lower biodiversity losses compared to pastures and conventional agriculture. This provides evidence that human-modified forests might still hold some forest specialist species compared with agricultural systems. For instance, agroforestry systems are recognized less impactful on biodiversity than conventional agricultural systems (Bhagwat et al., 2008; Udawatta et al., 2021). Maintaining different tree species in these production systems increases environmental heterogeneity (Edwards et al., 2014; Gómez-Cifuentes et al., 2019; Reis et al., 2023) and supports more diverse biological communities (Gómez-Cifuentes et al., 2020; Udawatta et al., 2021). Thus our findings bring insights that silvicultural systems can maintain higher

biodiversity levels than conventional agricultural systems (Derhé et al., 2016; Falcão et al., 2015; López-Bedoya et al., 2022; Romanelli et al., 2022) and thus are an important productive alternative to mitigate biodiversity loss.

Prioritizing these guidelines for the conservation and management of native forests, while promoting the conversion of agricultural and degraded areas into efficient and low-impact production systems (e.g., agroforestry), should be a long-term public policy of the State. These activities should also be subsidized and rewarded so that, as occurs with royalties from the production of minerals and oil in Brazil (Machado et al., 2012; Silva et al., 2021). That is, a financial compensation for municipalities, states, and agricultural producers that choose to maintain conserved areas and low-impact production activities. Technological, logistical, and educational support from government and non-governmental agencies should also be directed to farmers who adopt these guidelines instead of conventional practices. In addition, we should aim to put "the biodiversity of agricultural lands in the hands and minds of farmers" (Snoo et al., 2013) so that the goal of conserving biodiversity is not only financial, but becomes part of the agricultural culture. After all, even though financial incentives can contribute to conservation, the commercial nature of agricultural production does not ensure the continuity of conservation in the face of more financially attractive offers (Snoo et al., 2013). Thus, building a community culture in which biodiversity itself is the main reward for conservation is a complex but indispensable path to maintaining biodiversity.

Conclusion

Our study demonstrates the significant impact of land-use changes on Amazonian dung beetles and reinforces the importance of implementing conservation strategies to protect primary forests, sustainably manage selectively logged forests and adopt more heterogeneous production systems (e.g., agroforestry) to restore biodiversity within degraded areas. The implementation of these strategies should be included in national public policy, in order to encourage and assist rural producers, states, and municipalities to adopt them. In addition, encouraging less impactful production and conserving native forests should be planned in a way that is culturally integrated with communities and agricultural producers. By implementing these strategies, it may be possible to mitigate the negative effects of habitat conversion and contribute to the conservation of Amazonian biodiversity.

Our work also highlights the influence of land-use changes on biodiversity loss in the Amazon region. While providing valuable insights, our findings represent only a fraction of the complex ecological dynamics happening within tropical regions. Continued research efforts are necessary to

deepen our understanding of biodiversity response to anthropogenic changes and to contribute to evidence-based conservation strategies.

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3. CONCLUSÃO

Nosso estudo demonstra o impacto significativo das mudanças no uso da terra sobre os besouros rola-bosta da Amazônia e reforça a importância de implementar estratégias de conservação para proteger florestas primárias, gerenciar de forma sustentável florestas exploradas seletivamente e adotar sistemas de produção mais heterogêneos (por exemplo, agrofloresta) para restaurar a biodiversidade em áreas degradadas. A implementação dessas estratégias deve ser incluída como política pública nacional, a fim de estimular e apoiar produtores rurais, estados e municípios a adotá-las. Além disso, o estímulo a formas de produção agrícola de menor impacto e conservação de florestas nativas devem ser planejados e executados de forma a se integrar à cultura das comunidades e de produtores agrícolas. Ao implementar essas estratégias, pode ser possível mitigar os efeitos negativos da conversão de habitat e contribuir para a conservação da biodiversidade amazônica.

Nosso trabalho também destaca a influência das mudanças no uso da terra na perda de biodiversidade na região amazônica e embora forneça informações valiosas, nossas descobertas representam apenas uma fração da complexa dinâmica ecológica que acontece nas regiões tropicais. Esforços contínuos de pesquisa são necessários para aprofundar nossa compreensão da resposta da biodiversidade às mudanças antropogênicas e contribuir para estratégias de monitoramento e conservação baseadas em evidências.

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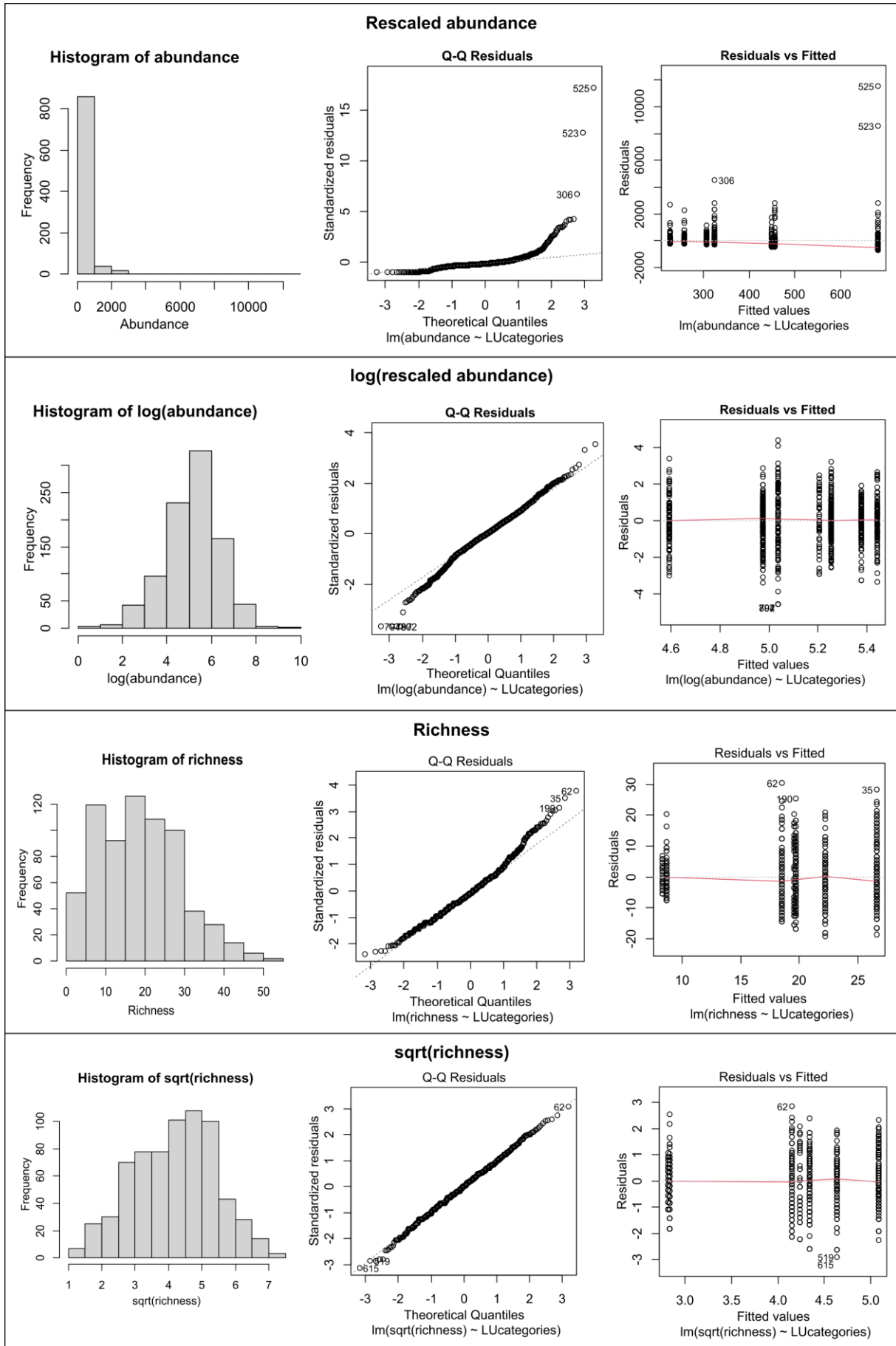
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ANEXO A - Avaliação dos pressupostos e transformação dos dados



ANEXO B – Lista de abundâncias total das espécies e morfoespécies por usos do solo.

Espécies/Morfoespécies	Usos do solo						
	Agricultura AG	Corte Seletivo SL	Fogo FF	Pastagem PA	Floresta Primária PF	Floresta Secundária SF	Silvicultura SI
<i>Agamopus_sp.1_21</i>	0	0	0	0	2	0	0
<i>Agamopus_sp.1_26</i>	0	0	0	68	6	0	0
<i>Anomiopus_aff._foveicollis_14</i>	0	1	0	0	0	1	0
<i>Anomiopus_aff._latistriatus_14</i>	0	0	0	0	0	1	0
<i>Anomiopus_aff._lunatipes_14</i>	0	0	0	0	0	1	0
<i>Anomiopus_aff._pereirai</i>	0	0	0	0	0	1	0
<i>Anomiopus_aff._pictus_14</i>	0	0	3	1	0	1	0
<i>Anomiopus_aff._smaragdinus_14</i>	0	1	0	0	0	3	0
<i>Anomiopus_batesii</i>	0	0	0	0	1	0	0
<i>Anomiopus_brevipes</i>	0	0	3	0	0	0	0
<i>Anomiopus_parallelus</i>	0	0	2	0	0	0	0
<i>Anomiopus_sp.1_14</i>	0	0	1	0	0	0	0
<i>Anomiopus_sp.1_26</i>	0	0	0	0	2	0	0
<i>Anomiopus_sp.1_30</i>	0	0	1	0	0	0	0
<i>Anomiopus_sp.1_31</i>	0	0	1	0	0	0	0
<i>Anomiopus_sp.2_14</i>	0	0	0	0	0	1	0
<i>Anomiopus_sp.3_14</i>	0	0	1	0	0	0	0
<i>Ateuchus_aff._aenomicans_14</i>	0	0	0	0	1	0	0
<i>Ateuchus_aff._candezei</i>	0	110	316	0	63	133	1
<i>Ateuchus_aff._connexus</i>	0	0	28	0	858	570	221
<i>Ateuchus_aff._latus_26</i>	0	0	0	430	12185	0	0
<i>Ateuchus_aff._murrayi</i>	0	3019	784	0	1860	578	48
<i>Ateuchus_aff._romani_14</i>	0	6	11	0	7	1	0
<i>Ateuchus_aff._semicribratus_26</i>	0	0	0	200	262	0	0
<i>Ateuchus_aff._steinbachi_26</i>	0	0	0	8	1	0	0
<i>Ateuchus_aff._striatulus</i>	0	0	13	5	211	2	0
<i>Ateuchus_aff._substriatus_21</i>	0	0	0	0	2	0	0
<i>Ateuchus_connexus</i>	0	357	60	0	230	48	0
<i>Ateuchus_irinus</i>	0	2	0	0	2016	1	194
<i>Ateuchus_pauki</i>	0	30	0	0	156	0	10
<i>Ateuchus_pygidialis</i>	0	1	1	841	41	0	0
<i>Ateuchus_sp.1_14</i>	0	44	146	0	69	76	0
<i>Ateuchus_sp.1_21</i>	0	0	0	0	25	0	0
<i>Ateuchus_sp.1_24</i>	0	0	0	0	0	111	0
<i>Ateuchus_sp.1_28</i>	0	0	41	0	55	0	0
<i>Ateuchus_sp.1_29</i>	0	0	2	0	1	0	0
<i>Ateuchus_sp.1_3</i>	0	0	0	0	2	4	380
<i>Ateuchus_sp.1_30</i>	0	0	7	0	12	0	0
<i>Ateuchus_sp.1_31</i>	0	0	7	0	0	0	0
<i>Ateuchus_sp.1_7</i>	0	0	0	0	300	0	501
<i>Ateuchus_sp.2_14</i>	0	11	78	0	3	8	0
<i>Ateuchus_sp.2_21</i>	0	0	0	0	9	0	0
<i>Ateuchus_sp.2_24</i>	0	0	0	1	0	1288	0
<i>Ateuchus_sp.2_3</i>	0	0	0	0	0	1	0
<i>Ateuchus_sp.2_30</i>	0	0	151	0	61	0	0
<i>Ateuchus_sp.2_7</i>	0	0	0	0	4	0	1
<i>Ateuchus_sp.3_14</i>	0	485	393	0	19	77	0
<i>Ateuchus_sp.3_24</i>	0	0	0	1	0	519	0
<i>Ateuchus_sp.3_7</i>	0	0	0	0	43	0	14
<i>Ateuchus_sp.4_14</i>	0	0	0	0	3	0	0

Espécies/Morfoespécies	AG	SL	FF	PA	PF	SF	SI
<i>Ateuchus_sp.4_24</i>	0	0	0	0	0	116	0
<i>Ateuchus_sp.4_29</i>	0	0	4	0	2	0	0
<i>Ateuchus_sp.4_7</i>	0	0	0	0	73	0	4
<i>Ateuchus_sp.5_14</i>	0	10	20	0	12	1	0
<i>Ateuchus_sp.5_24</i>	0	0	0	0	0	63	0
<i>Ateuchus_sp.5_3</i>	0	0	0	0	1	0	0
<i>Ateuchus_sp.5_7</i>	0	0	0	0	17	0	2
<i>Ateuchus_sp.6_14</i>	0	0	1	0	4	0	0
<i>Ateuchus_sp.6_24</i>	0	0	0	0	0	11	0
<i>Ateuchus_sp.6_7</i>	0	0	0	0	71	0	1
<i>Ateuchus_sp.7_14</i>	0	0	12	0	0	0	0
<i>Ateuchus_sp.7_3</i>	0	0	0	0	1	0	0
<i>Ateuchus_sp.7_7</i>	0	0	0	0	6	0	0
<i>Ateuchus_sp.8_14</i>	0	0	1	0	0	0	0
<i>Ateuchus_striatulus</i>	0	0	1	0	0	0	0
<i>Ateuchus_substriatus</i>	0	0	1	0	2	0	0
<i>Ateuchus_vividus</i>	0	0	0	3	0	0	0
<i>Bdelyrus_paraensis</i>	0	2	11	0	6	0	0
<i>Bdelyrus_sp.1_14</i>	0	1	0	0	0	1	0
<i>Besourenga_horacioi</i>	0	0	4	0	1	0	0
<i>Canthidium_aeneolum</i>	0	0	0	3	1	0	0
<i>Canthidium_aff.ardens</i>	108	41	821	226	50	579	7
<i>Canthidium_aff.barbacenicum</i>	200	21	95	710	44	248	53
<i>Canthidium_aff.basale_26</i>	0	0	0	0	8	0	0
<i>Canthidium_aff.collare_14</i>	0	39	107	0	29	195	3
<i>Canthidium_aff.cupreum</i>	0	0	114	1	60	0	0
<i>Canthidium_aff.depressum</i>	0	0	17	0	24	0	0
<i>Canthidium_aff.deyrollei</i>	0	68	1896	0	1182	1252	9
<i>Canthidium_aff.dohrni_3</i>	0	0	0	0	1	0	0
<i>Canthidium_aff.funebre</i>	0	3	2	0	5	0	0
<i>Canthidium_aff.gerstaeckeri</i>	0	187	221	2	433	68	4
<i>Canthidium_aff.gerstaeckeri_sp.1_30</i>	0	0	3	0	0	0	0
<i>Canthidium_aff.gerstaeckeri_sp.2_30</i>	0	0	3	0	2	0	0
<i>Canthidium_aff.humerale_29</i>	0	0	36	0	0	0	0
<i>Canthidium_aff.lentum</i>	31	105	384	26	296	223	577
<i>Canthidium_aff.lentum_sp.1_30</i>	0	0	8	0	1	0	0
<i>Canthidium_aff.lentum_sp.2_30</i>	0	0	0	0	2	0	0
<i>Canthidium_aff.lentum_sp.3_30</i>	0	0	36	0	8	0	0
<i>Canthidium_aff.multipunctatum_29</i>	0	0	2	0	0	0	0
<i>Canthidium_aff.pullum_26</i>	0	0	0	1	0	0	0
<i>Canthidium_angulicolle</i>	0	0	0	618	36	0	0
<i>Canthidium_funebre</i>	0	1	0	0	10	0	0
<i>Canthidium_humerale</i>	35	11	8	203	2	18	20
<i>Canthidium_metallicum</i>	0	0	1	0	4	0	0
<i>Canthidium_multipunctatum</i>	53	1	0	91	2	24	2
<i>Canthidium_onitoides</i>	0	0	0	0	1	0	0
<i>Canthidium_pinotoides</i>	0	0	0	471	860	0	0
<i>Canthidium_semicupreum</i>	0	25	13	1	5	1	0
<i>Canthidium_sp.1_14</i>	1	190	331	5	182	227	1
<i>Canthidium_sp.1_21</i>	25	0	0	0	3	0	0
<i>Canthidium_sp.1_24</i>	0	0	0	0	0	252	0
<i>Canthidium_sp.1_28</i>	0	0	1	0	6	0	0
<i>Canthidium_sp.1_3</i>	0	0	0	0	1	0	0
<i>Canthidium_sp.1_30</i>	0	0	81	0	9	0	0
<i>Canthidium_sp.1_31</i>	0	0	1	0	0	0	0
<i>Canthidium_sp.1_7</i>	0	4	0	0	37	0	1
<i>Canthidium_sp.10_14</i>	0	1	0	0	5	1	1
<i>Canthidium_sp.10_26</i>	0	0	0	29	2	0	0
<i>Canthidium_sp.10_7</i>	0	0	0	0	2	0	1

Espécies/Morfoespécies	AG	SL	FF	PA	PF	SF	SI
<i>Canthidium_sp.11_14</i>	2	0	2	2	0	0	0
<i>Canthidium_sp.11_24</i>	0	0	0	0	0	1	0
<i>Canthidium_sp.11_26</i>	0	0	0	11	1271	0	0
<i>Canthidium_sp.11_3</i>	0	0	0	0	2	0	0
<i>Canthidium_sp.11_7</i>	0	46	0	0	58	0	3
<i>Canthidium_sp.12_24</i>	0	0	0	0	0	1	0
<i>Canthidium_sp.12_26</i>	0	0	0	0	50	0	0
<i>Canthidium_sp.12_3</i>	0	0	0	0	0	0	3
<i>Canthidium_sp.12_7</i>	0	0	0	0	13	0	105
<i>Canthidium_sp.13_26</i>	0	0	0	1	126	0	0
<i>Canthidium_sp.13_3</i>	0	0	0	0	3	0	0
<i>Canthidium_sp.13_7</i>	0	38	0	0	93	0	0
<i>Canthidium_sp.14_26</i>	0	0	0	0	5	0	0
<i>Canthidium_sp.14_3</i>	0	0	0	0	1	0	0
<i>Canthidium_sp.15_26</i>	0	0	0	1	14	0	0
<i>Canthidium_sp.15_7</i>	0	0	0	0	6	0	0
<i>Canthidium_sp.16_14</i>	0	0	0	0	1	0	0
<i>Canthidium_sp.2_14</i>	16	28	68	53	13	82	0
<i>Canthidium_sp.2_21</i>	0	0	0	0	1	0	0
<i>Canthidium_sp.2_24</i>	0	0	0	0	0	46	0
<i>Canthidium_sp.2_26</i>	0	0	0	132	4	0	0
<i>Canthidium_sp.2_3</i>	0	0	0	0	3	0	0
<i>Canthidium_sp.2_30</i>	0	0	53	0	1	0	0
<i>Canthidium_sp.2_31</i>	0	0	1	0	0	0	0
<i>Canthidium_sp.2_7</i>	0	40	0	0	289	0	1
<i>Canthidium_sp.20_14</i>	0	1	0	0	1	0	0
<i>Canthidium_sp.21_14</i>	0	1	11	0	1	7	0
<i>Canthidium_sp.22_14</i>	0	0	3	0	0	2	0
<i>Canthidium_sp.23_14</i>	0	1	1	0	0	0	0
<i>Canthidium_sp.24_14</i>	0	0	0	0	1	0	0
<i>Canthidium_sp.25_14</i>	0	0	0	0	0	1	0
<i>Canthidium_sp.3_14</i>	1	0	11	0	3	30	6
<i>Canthidium_sp.3_21</i>	90	0	0	0	51	0	0
<i>Canthidium_sp.3_24</i>	0	0	0	6	0	99	0
<i>Canthidium_sp.3_28</i>	0	0	5	0	8	0	0
<i>Canthidium_sp.3_30</i>	0	0	2	0	0	0	0
<i>Canthidium_sp.3_31</i>	0	0	1	0	0	0	0
<i>Canthidium_sp.4_14</i>	0	211	55	0	55	102	0
<i>Canthidium_sp.4_21</i>	1	0	0	0	1	0	0
<i>Canthidium_sp.4_24</i>	0	0	0	1	0	11	0
<i>Canthidium_sp.4_26</i>	0	0	0	2	502	0	0
<i>Canthidium_sp.4_28</i>	0	0	1	0	1	0	0
<i>Canthidium_sp.4_3</i>	0	0	0	0	1	0	0
<i>Canthidium_sp.4_30</i>	0	0	2	0	1	0	0
<i>Canthidium_sp.4_7</i>	0	10	0	0	38	0	27
<i>Canthidium_sp.5_14</i>	1	578	751	4	74	165	47
<i>Canthidium_sp.5_24</i>	0	0	0	0	0	2	0
<i>Canthidium_sp.5_28</i>	0	0	0	0	3	0	0
<i>Canthidium_sp.5_30</i>	0	0	8	0	0	0	0
<i>Canthidium_sp.6_14</i>	0	26	0	0	2	18	0
<i>Canthidium_sp.6_24</i>	0	0	0	0	0	2	0
<i>Canthidium_sp.6_30</i>	0	0	390	0	5	0	0
<i>Canthidium_sp.6_7</i>	0	0	0	0	21	0	2
<i>Canthidium_sp.7_14</i>	0	4	11	1	1	14	0
<i>Canthidium_sp.7_24</i>	0	0	0	0	0	1	0
<i>Canthidium_sp.7_26</i>	0	0	0	2	21	0	0
<i>Canthidium_sp.7_28</i>	0	0	4	0	3	0	0
<i>Canthidium_sp.7_3</i>	0	0	0	0	9	0	0
<i>Canthidium_sp.7_30</i>	0	0	10	0	0	0	0

Espécies/Morfoespécies	AG	SL	FF	PA	PF	SF	SI
<i>Canthidium_sp.7_7</i>	0	30	0	0	56	0	24
<i>Canthidium_sp.8_14</i>	0	137	305	0	148	24	0
<i>Canthidium_sp.8_24</i>	0	0	0	0	0	1	0
<i>Canthidium_sp.8_3</i>	0	0	0	0	7	1	0
<i>Canthidium_sp.8_7</i>	0	20	0	0	82	0	5
<i>Canthidium_sp.9_14</i>	0	0	0	0	25	0	0
<i>Canthidium_sp.9_24</i>	0	0	0	0	0	2	0
<i>Canthidium_sp.9_7</i>	0	0	0	0	46	0	19
<i>Canthidium_tricolor</i>	0	0	0	0	3	0	0
<i>Canthon_aff._acutus</i>	1033	0	0	352	1	143	231
<i>Canthon_aff._angustatus</i>	0	75	49	0	72	11	0
<i>Canthon_aff._chalybaeus</i>	184	0	5	62	266	233	222
<i>Canthon_aff._chiriguano_26</i>	0	0	0	1	47	0	0
<i>Canthon_aff._coloratus_26</i>	0	0	0	0	6	0	0
<i>Canthon_aff._gerstaeckeri_3</i>	0	0	0	0	1	0	0
<i>Canthon_aff._heyrovskyi</i>	297	0	2	344	0	114	116
<i>Canthon_aff._juvencus_28</i>	0	0	0	0	1	0	0
<i>Canthon_aff._marmoratus_26</i>	0	0	0	3	50	0	0
<i>Canthon_aff._octodentatus_14</i>	0	0	0	8	0	0	6
<i>Canthon_aff._pilluliformis_29</i>	0	0	17	0	1	0	0
<i>Canthon_aff._quadriguttatus_30</i>	0	0	53	0	2	0	0
<i>Canthon_aff._quadrimaculatus_14</i>	0	51	43	0	12	392	0
<i>Canthon_aff._quinquemaculatus</i>	0	0	36	0	24	0	0
<i>Canthon_aff._rufocoeruleus_26</i>	0	0	0	0	1	0	0
<i>Canthon_aff._scrutator</i>	0	0	21	0	0	0	0
<i>Canthon_aff._simulans</i>	60	3	16	471	1	165	26
<i>Canthon_aff._subhyalinus</i>	0	0	27	0	5	0	0
<i>Canthon_aff._triangularis_26</i>	0	0	0	2	797	0	0
<i>Canthon_aff._xanthopus</i>	0	63	25	13	7	40	0
<i>Canthon_bicolor</i>	0	0	0	0	105	0	5
<i>Canthon_bimaculatus</i>	0	0	0	0	484	0	0
<i>Canthon_brunneus</i>	0	0	0	0	299	0	0
<i>Canthon_chalybaeus</i>	0	0	1	4	0	49	0
<i>Canthon_cinctellus</i>	0	0	0	47	0	0	0
<i>Canthon_conformis</i>	431	0	0	0	4	0	0
<i>Canthon_curvodilatatus</i>	0	0	0	110	1	0	0
<i>Canthon_dives</i>	0	0	0	12	0	0	0
<i>Canthon_fulgidus</i>	0	2574	1949	1	1147	1212	0
<i>Canthon_granuliceps</i>	0	0	0	1	0	0	0
<i>Canthon_hendrichsi</i>	0	0	0	1	0	0	0
<i>Canthon_histrio</i>	26	0	153	225	650	510	24
<i>Canthon_lituratus</i>	543	0	91	1351	16	169	587
<i>Canthon_luteicollis</i>	0	0	67	0	79	0	0
<i>Canthon_mutabilis</i>	0	0	0	5	0	0	1
<i>Canthon_quadriguttatus</i>	0	10	1	0	363	1	17
<i>Canthon_quadrimaculatus</i>	0	0	0	0	0	3	0
<i>Canthon_quinquemaculatus</i>	0	0	0	0	28	0	0
<i>Canthon_rufocoeruleus</i>	0	45	35	6	0	16	0
<i>Canthon_scrutator</i>	266	0	35	239	24	65	299
<i>Canthon_semiopacus</i>	0	4	8	0	26	0	0
<i>Canthon_simulans</i>	0	0	0	0	20	1	1283
<i>Canthon_sp.1_14</i>	3	0	0	12	0	1	24
<i>Canthon_sp.1_26</i>	0	0	0	2	0	0	0
<i>Canthon_sp.1_29</i>	0	0	1	0	0	0	0
<i>Canthon_sp.1_31</i>	0	0	1	0	0	0	0
<i>Canthon_sp.13_30</i>	0	0	0	0	12	0	0
<i>Canthon_subhyalinus</i>	0	0	0	0	346	483	19
<i>Canthon_triangularis</i>	0	238	13	6	1693	586	353
<i>Canthon_xanthopus</i>	0	0	0	0	0	1	0

Espécies/Morfoespécies	AG	SL	FF	PA	PF	SF	SI
<i>Canthonella_sp.1_14</i>	0	2	1	0	0	0	0
<i>Canthonella_sp.1_24</i>	0	0	0	0	0	4	0
<i>Canthonella_sp.1_25</i>	0	0	0	26	0	0	0
<i>Canthonella_sp.1_26</i>	0	0	0	1	83	0	0
<i>Canthonella_sp.1_30</i>	0	0	48	0	3	0	0
<i>Canthonella_sp.1_7</i>	0	36	0	0	17	0	0
<i>Canthonella_sp.2_14</i>	0	0	1	0	0	0	0
<i>Coprophanaeus_aff_ensifer</i>	0	0	11	1	20	0	0
<i>Coprophanaeus_cyanescens</i>	3	0	0	0	113	0	0
<i>Coprophanaeus_dardanus</i>	4	0	22	1	30	13	3
<i>Coprophanaeus_degallieri</i>	8	8	4	49	18	0	1
<i>Coprophanaeus_jasius</i>	1	12	7	0	29	4	1
<i>Coprophanaeus_lancifer</i>	9	183	186	0	249	106	42
<i>Coprophanaeus_sp.4_28</i>	0	0	5	0	8	0	0
<i>Coprophanaeus_spitzi</i>	0	0	0	2	5	0	0
<i>Coprophanaeus_telamon</i>	0	0	0	0	33	0	0
<i>Cryptocanthon_campbellorum</i>	0	64	30	0	11	4	0
<i>Cryptocanthon_pectorum</i>	0	58	23	0	33	9	0
<i>Cryptocanthon_sp.1_29</i>	0	0	0	0	1	0	0
<i>Deltochilum_aff_chalcea_31</i>	0	0	24	0	0	0	0
<i>Deltochilum_aff_crenulipes_26</i>	0	0	0	2	20	0	0
<i>Deltochilum_aff_guyanense_21</i>	0	0	0	0	2	0	0
<i>Deltochilum_aff_komareki_26</i>	0	0	0	1	69	0	0
<i>Deltochilum_aff_orbignyi</i>	0	0	26	0	28	0	0
<i>Deltochilum_aff_peruanum</i>	0	0	0	0	226	385	276
<i>Deltochilum_aff_sextuberculatum_14</i>	0	18	74	0	3	9	0
<i>Deltochilum_aff_submetallicum</i>	0	262	0	0	734	9	44
<i>Deltochilum_carinatum</i>	0	24	2	0	45	0	0
<i>Deltochilum_chalcea</i>	0	0	2	0	8	0	0
<i>Deltochilum_enceladus</i>	0	120	80	0	335	18	0
<i>Deltochilum_guildingii</i>	0	0	0	0	4	0	1
<i>Deltochilum_icarus</i>	0	40	24	0	145	4	8
<i>Deltochilum_orbicolare</i>	0	321	67	0	184	30	2
<i>Deltochilum_orbignyi</i>	0	29	15	0	25	17	0
<i>Deltochilum_pseudoicarus</i>	0	0	0	1	0	0	0
<i>Deltochilum_schefflerorum</i>	0	5	0	0	0	0	0
<i>Deltochilum_septemstriatum</i>	0	0	0	0	103	0	14
<i>Deltochilum_sextuberculatum</i>	0	0	0	0	26	0	0
<i>Deltochilum_sp.1_14</i>	0	222	322	0	34	46	0
<i>Deltochilum_sp.1_21</i>	0	0	0	0	35	0	0
<i>Deltochilum_sp.1_24</i>	0	0	0	0	0	22	0
<i>Deltochilum_sp.1_28</i>	0	0	5	0	17	0	0
<i>Deltochilum_sp.1_29</i>	0	0	1	0	2	0	0
<i>Deltochilum_sp.1_3</i>	0	0	0	0	4	0	0
<i>Deltochilum_sp.1_30</i>	0	0	1	0	5	0	0
<i>Deltochilum_sp.1_7</i>	0	0	0	0	16	0	0
<i>Deltochilum_sp.2_14</i>	0	535	589	0	280	287	0
<i>Deltochilum_sp.2_24</i>	0	0	0	0	0	1	0
<i>Deltochilum_sp.2_3</i>	0	0	0	0	1	0	0
<i>Deltochilum_sp.2_30</i>	0	0	3	0	20	0	0
<i>Deltochilum_sp.2_7</i>	0	0	0	0	22	0	0
<i>Deltochilum_sp.7_28</i>	0	0	0	0	1	0	0
<i>Deltorhinum_kempffmercadoi</i>	0	0	0	0	1	0	0
<i>Dendropaemon_aff_refulgens_14</i>	0	0	0	0	0	1	0
<i>Dendropaemon_sp.1_7</i>	0	0	0	0	1	0	0
<i>Diabroctis_mimas</i>	170	5	67	1341	2	61	132
<i>Dichotomius_aff_batesi</i>	0	16	5	0	15	30	0
<i>Dichotomius_aff_clypeatus_30</i>	0	0	0	0	2	0	0
<i>Dichotomius_aff_crenatipennis_26</i>	0	0	0	0	28	0	0

Espécies/Morfoespécies	AG	SL	FF	PA	PF	SF	SI
<i>Dichotomius aff. depressum</i> 31	0	0	1	0	0	0	0
<i>Dichotomius aff. fortistriatus</i> 14	0	368	550	0	171	520	0
<i>Dichotomius aff. globulus</i>	0	1540	1372	4	538	299	0
<i>Dichotomius aff. lucasi</i>	0	343	1282	2	2884	1154	160
<i>Dichotomius aff. lucasi sp.1</i> 14	0	5	0	0	1	0	0
<i>Dichotomius aff. lucasi sp.1</i> 26	0	0	0	0	740	0	0
<i>Dichotomius aff. lucasi sp.2</i> 14	0	10	11	0	24	0	0
<i>Dichotomius aff. lucasi sp.2</i> 26	0	0	0	0	771	0	0
<i>Dichotomius aff. melzeri</i> 24	0	0	0	0	0	4	0
<i>Dichotomius aff. tristis</i> 31	0	0	55	0	0	0	0
<i>Dichotomius aff. worontzowi</i>	0	0	0	0	3	0	0
<i>Dichotomius apicalis</i>	0	758	0	0	1268	5	22
<i>Dichotomius boreus</i>	0	431	305	0	896	36	33
<i>Dichotomius bos</i>	2	0	0	634	193	0	0
<i>Dichotomius carinatus</i>	2	111	94	0	118	113	0
<i>Dichotomius conicollis</i>	0	0	21	0	18	0	0
<i>Dichotomius gr. fissus</i> 29	0	0	0	0	3	0	0
<i>Dichotomius gr. selenocopris sp.1</i> 26	0	0	0	0	1	0	0
<i>Dichotomius gr. selenocopris sp.2</i> 26	0	0	0	0	1	0	0
<i>Dichotomius inachus</i>	0	85	49	1	0	54	0
<i>Dichotomius latilobatus</i>	0	38	0	0	101	6	637
<i>Dichotomius longiceps</i>	0	0	0	0	0	3	6
<i>Dichotomius lucasi</i>	0	86	20	0	46	0	0
<i>Dichotomius lycas</i>	0	0	0	12	46	0	0
<i>Dichotomius mamillatus</i>	0	0	55	0	339	75	18
<i>Dichotomius melzeri</i>	1	53	189	1	162	73	4
<i>Dichotomius nimuendaju</i>	0	0	0	0	6	0	0
<i>Dichotomius nisus</i>	394	0	41	1839	239	104	17
<i>Dichotomius ohausi</i>	0	0	2	0	3	0	0
<i>Dichotomius opacipennis</i>	0	0	0	0	20	0	0
<i>Dichotomius opacus</i>	0	0	0	25	3031	0	0
<i>Dichotomius prietoi</i>	0	0	39	0	32	1	0
<i>Dichotomius pseudocuprinus</i>	0	0	0	14	21	0	0
<i>Dichotomius robustus</i>	0	3	20	0	22	13	2
<i>Dichotomius semiaeneus</i>	0	0	0	13	0	0	0
<i>Dichotomius sp.1</i> 14	0	1	2	0	0	0	0
<i>Dichotomius sp.1</i> 31	0	0	1	0	0	0	0
<i>Dichotomius sp.1</i> 7	0	0	0	0	3	0	0
<i>Dichotomius sp.12</i> 28	0	0	1	0	1	0	0
<i>Dichotomius sp.2</i> 31	0	0	1	0	0	0	0
<i>Dichotomius sp.3</i> 31	0	0	1	0	0	0	0
<i>Dichotomius subaeneus</i>	0	428	0	0	487	1	10
<i>Dichotomius telamon</i>	0	23	42	0	1	15	0
<i>Dichotomius worontzowi</i>	1	103	103	0	104	78	38
<i>Digitonthophagus gazella</i>	119	7	1	1024	0	1	7
<i>Eurysternus aff. hypocrita</i> 28	0	0	17	0	14	0	0
<i>Eurysternus aff. vastiorum</i> 28	0	0	0	0	4	0	0
<i>Eurysternus arnaudi</i>	0	55	13	1	25	216	0
<i>Eurysternus atrosericus</i>	0	1831	1179	3	3880	1299	116
<i>Eurysternus balachowskyi</i>	0	57	27	0	91	77	4
<i>Eurysternus caribaeus</i>	0	3035	1762	5	8961	1077	212
<i>Eurysternus cavatus</i>	0	88	110	0	12	5	0
<i>Eurysternus cayennensis</i>	0	203	96	0	306	11	1
<i>Eurysternus cyclops</i>	0	9	1	0	11	0	1
<i>Eurysternus foedus</i>	0	489	37	2	353	166	25
<i>Eurysternus gracilis</i>	0	0	0	0	0	9	0
<i>Eurysternus hamaticollis</i>	0	81	44	0	61	35	3
<i>Eurysternus harlequin</i>	0	1	0	0	1	0	0
<i>Eurysternus howdeni</i>	0	5	3	0	7	0	0

Espécies/Morfoespécies	AG	SL	FF	PA	PF	SF	SI
<i>Eurysternus_hypocrita</i>	0	26	7	0	268	38	8
<i>Eurysternus_jessopi</i>	0	4	0	0	6	0	0
<i>Eurysternus_plebejus</i>	0	37	41	0	93	16	0
<i>Eurysternus_sp.1_28</i>	0	0	1	0	3	0	0
<i>Eurysternus_sp.1_7</i>	0	0	0	0	2	0	0
<i>Eurysternus_sp.2_28</i>	0	0	1	0	2	0	0
<i>Eurysternus_strigilatus</i>	0	0	0	0	124	38	2
<i>Eurysternus_vastiorum</i>	0	8	43	0	182	19	73
<i>Eurysternus_ventricosus</i>	0	235	5	0	101	42	24
<i>Eurysternus_wittmerorum</i>	0	708	502	0	1268	813	0
<i>Eutrichillum_sp.1_14</i>	0	3	2	0	1	3	0
<i>Eutrichillum_sp.1_26</i>	0	0	0	1	7	0	0
<i>Eutrichillum_sp.1_7</i>	0	0	0	0	1	0	0
<i>Genieridium_bidens</i>	0	0	0	917	5	0	0
<i>Genieridium_cryptops</i>	0	0	22	6	99	0	0
<i>Hansreia_affinis</i>	0	152	5	0	16	17	0
<i>Hansreia_oxygona</i>	0	0	7	0	93	0	0
<i>Hansreia_sp.1_24</i>	0	0	0	0	0	118	0
<i>Isocopris_aff_imitator_29</i>	0	0	13	0	7	0	0
<i>Isocopris_imitator</i>	0	12	43	0	46	32	32
<i>Isocopris_nitidus</i>	0	1	2	0	0	0	0
<i>Malagoniella_aff_punctatostriata_26</i>	0	0	0	0	5	0	0
<i>Malagoniella_astyanax</i>	0	0	14	0	0	0	0
<i>Malagoniella_sp.1_28</i>	0	0	0	0	5	0	0
<i>Ontherus_appendiculatus</i>	8	0	221	626	42	23	1
<i>Ontherus_azteca</i>	0	0	26	0	49	0	0
<i>Ontherus_cambeforti</i>	0	0	0	0	2	0	2
<i>Ontherus_carinifrons</i>	0	0	126	0	524	49	2734
<i>Ontherus_digitatus</i>	0	0	0	1	8	0	0
<i>Ontherus_planus</i>	0	0	0	0	1	0	0
<i>Ontherus_pubens</i>	0	0	52	0	92	0	0
<i>Ontherus_sp.1_29</i>	0	0	1	0	0	0	0
<i>Ontherus_sp.1_31</i>	0	0	1	0	0	0	0
<i>Ontherus_sulcator</i>	72	12	358	287	49	179	439
<i>Ontherus_ulcopygus</i>	0	0	0	1	0	0	0
<i>Onthophagus_aff_bidentatus</i>	2	0	8	0	656	669	1249
<i>Onthophagus_aff_buculus</i>	0	0	0	319	1	0	0
<i>Onthophagus_aff_clypeatus</i>	0	0	8	0	111	4	10
<i>Onthophagus_aff_haematopus</i>	0	0	15	7	964	2186	41
<i>Onthophagus_aff_hirculus</i>	371	265	162	671	195	140	238
<i>Onthophagus_aff_marginicollis</i>	0	0	0	0	7	1	235
<i>Onthophagus_aff_onorei</i>	0	1	13	0	9	5	0
<i>Onthophagus_aff_osculatii</i>	0	0	14	0	59	0	0
<i>Onthophagus_aff_rubrescens_21</i>	4	0	0	0	58	0	0
<i>Onthophagus_bidentatus</i>	0	2644	254	0	1454	0	0
<i>Onthophagus_onthochromus</i>	0	29	8	9	15	15	4
<i>Onthophagus_osculatii</i>	3	454	336	12	93	268	17
<i>Onthophagus_ptox</i>	0	2	0	0	0	0	0
<i>Onthophagus_rubrescens</i>	4	3373	1141	66	3303	340	0
<i>Onthophagus_sp.1_14</i>	7	923	950	1	830	811	0
<i>Onthophagus_sp.1_21</i>	148	0	0	0	34	0	0
<i>Onthophagus_sp.1_26</i>	0	0	0	0	686	0	0
<i>Onthophagus_sp.1_28</i>	0	0	408	0	501	0	0
<i>Onthophagus_sp.1_31</i>	0	0	1	0	0	0	0
<i>Onthophagus_sp.2_14</i>	0	3	3	0	19	0	0
<i>Onthophagus_sp.2_31</i>	0	0	1	0	0	0	0
<i>Onthophagus_sp.3_14</i>	0	0	0	0	5	0	0
<i>Onthophagus_sp.3_31</i>	0	0	1	0	0	0	0
<i>Onthophagus_sp.4_31</i>	0	0	1	0	0	0	0

Espécies/Morfoespécies	AG	SL	FF	PA	PF	SF	SI
<i>Onthophagus_sp.5_14</i>	0	1	0	0	0	0	0
<i>Onthophagus_sp.5_31</i>	0	0	1	0	0	0	0
<i>Onthophagus_sp.6_31</i>	0	0	1	0	0	0	0
<i>Oxysternon_conspicillatum</i>	0	0	6	0	566	7	0
<i>Oxysternon_durantoni</i>	0	216	0	0	164	0	0
<i>Oxysternon_festivum</i>	0	116	112	0	3085	175	261
<i>Oxysternon_lautum</i>	0	0	4	0	0	0	0
<i>Oxysternon_macleayi</i>	0	290	308	0	472	121	0
<i>Oxysternon_palemo</i>	0	0	0	12	0	0	0
<i>Oxysternon_silenus</i>	0	56	63	0	86	18	6
<i>Oxysternon_spiniferum</i>	0	0	0	0	4	0	0
<i>Oxysternon_striatopunctatum</i>	0	0	0	0	0	1	0
<i>Phanaeus_bispinus</i>	0	0	1	0	5	0	1
<i>Phanaeus_bordoni</i>	0	0	1	0	0	0	0
<i>Phanaeus_cambeforti</i>	0	0	0	0	51	0	0
<i>Phanaeus_chalcomelas</i>	0	8	38	0	179	33	43
<i>Phanaeus_kirbyi</i>	0	0	0	1	0	0	0
<i>Phanaeus_palaeno</i>	0	0	0	2	0	0	0
<i>Phanaeus_sororibispinus</i>	2	0	2	0	4	0	0
<i>Pseudocanthon_aff._xanthurus</i>	0	0	0	5	5	0	132
<i>Pseudocanthon_sp.1_24</i>	0	0	0	15	0	0	0
<i>Pseudocanthon_xanthurus</i>	2425	1	14	4489	0	175	237
<i>Scatimus_simulator</i>	0	0	52	0	0	0	0
<i>Scybalocanthon_aereus</i>	0	0	0	0	1	0	0
<i>Scybalocanthon_sp.1_14</i>	0	7	26	0	4	4	0
<i>Scybalocanthon_sp.1_28</i>	0	0	6	0	7	0	0
<i>Scybalocanthon_sp.1_29</i>	0	0	20	0	20	0	0
<i>Scybalocanthon_sp.1_3</i>	0	0	0	0	7	0	2
<i>Scybalocanthon_sp.1_30</i>	0	0	25	0	139	0	0
<i>Scybalocanthon_sp.1_31</i>	0	0	7	0	0	0	0
<i>Scybalocanthon_sp.1_7</i>	0	0	0	0	4	0	59
<i>Scybalocanthon_sp.2_30</i>	0	0	8	0	2	0	0
<i>Scybalocanthon_uniplagiatus</i>	0	0	0	0	78	0	0
<i>Sinapisoma_sp.1_26</i>	0	0	0	1	0	0	0
<i>Sinapisoma_sp.1_7</i>	0	4	0	0	0	0	0
<i>Sulcophanaeus_faunus</i>	0	10	1	0	25	5	0
<i>Sylvicanthon_candezei</i>	0	0	0	0	5	0	0
<i>Sylvicanthon_proseni</i>	0	796	715	0	494	1130	0
<i>Sylvicanthon_sp.1_14</i>	2	2	65	0	1	221	0
<i>Sylvicanthon_sp.1_26</i>	0	0	0	0	586	0	0
<i>Sylvicanthon_sp.1_28</i>	0	0	9	0	7	0	0
<i>Sylvicanthon_sp.1_29</i>	0	0	5	0	14	0	0
<i>Sylvicanthon_sp.1_30</i>	0	0	562	0	147	0	0
<i>Sylvicanthon_sp.2_29</i>	0	0	3	0	14	0	0
<i>Sylvicanthon_sp.3_29</i>	0	0	2	0	2	0	0
<i>Tetraechma_liturata</i>	0	0	5	0	0	0	0
<i>Trichillidium_sp.1_3</i>	0	0	0	0	9	9	7
<i>Trichillidium_sp.1_7</i>	0	0	0	0	1	0	17
<i>Trichillum_aff._externepunctatum_28</i>	0	0	2	0	0	0	0
<i>Trichillum_externepunctatum</i>	932	11	176	16877	568	115	38
<i>Trichillum_pauliani</i>	0	3	93	0	257	13	3
<i>Trichillum_sp.1_14</i>	3481	15	1428	19563	42	263	174
<i>Trichillum_sp.3_7</i>	0	0	0	0	3	0	0
<i>Uroxys_aff._batesi_28</i>	0	0	2	0	2	0	0
<i>Uroxys_aff._besti_3</i>	0	0	0	0	0	1	0
<i>Uroxys_besti</i>	0	0	0	0	2	2	0
<i>Uroxys_sp.1_14</i>	2	79	165	2	56	64	0
<i>Uroxys_sp.1_21</i>	0	0	0	0	7	0	0
<i>Uroxys_sp.1_24</i>	0	0	0	0	0	9	0

Espécies/Morfoespécies	AG	SL	FF	PA	PF	SF	SI
<i>Uroxys_sp.1_26</i>	0	0	0	0	423	0	0
<i>Uroxys_sp.1_3</i>	0	0	0	0	141	1	13
<i>Uroxys_sp.1_30</i>	0	0	239	0	35	0	0
<i>Uroxys_sp.1_7</i>	0	0	0	0	29	0	14
<i>Uroxys_sp.2_14</i>	0	33	2	2	4	0	0
<i>Uroxys_sp.2_21</i>	0	0	0	0	8	0	0
<i>Uroxys_sp.2_24</i>	0	0	0	0	0	4	0
<i>Uroxys_sp.2_26</i>	0	0	0	0	816	0	0
<i>Uroxys_sp.2_3</i>	0	0	0	0	9	1	0
<i>Uroxys_sp.2_30</i>	0	0	3	0	6	0	0
<i>Uroxys_sp.2_7</i>	0	0	0	0	8	0	1
<i>Uroxys_sp.3_14</i>	0	12	4	0	3	9	0
<i>Uroxys_sp.3_21</i>	0	0	0	0	1	0	0
<i>Uroxys_sp.3_26</i>	0	0	0	0	22	0	0
<i>Uroxys_sp.3_3</i>	0	0	0	0	60	1	46
<i>Uroxys_sp.3_7</i>	0	198	0	0	2335	0	133
<i>Uroxys_sp.4_14</i>	0	5	9	0	2	2	0
<i>Uroxys_sp.4_21</i>	0	0	0	0	2	0	0
<i>Uroxys_sp.5_14</i>	0	0	0	0	2	0	0